# MAMMALIAN SPECIES No. 398, pp. 1-8, 3 figs.

### Myocastor coypus.

By Charles A. Woods, Luis Contreras, Gale Willner-Chapman, and Howard P. Whidden

Published 5 June 1992 by The American Society of Mammalogists

#### Myocastor Kerr, 1792

Myocastor Kerr, 1792:225. Type species Mus coypus Molina, 1782.

CONTEXT AND CONTENT. Order Rodentia, Family Myocastoridae. The genus *Myocastor* is monotypic as treated below, though myocastorids are sometimes classified as a subfamily of the Capromyidae (Hall, 1981; Simpson, 1945). Patterson and Pascual (1968) and Patterson and Wood (1982) consider both myocastorids and capromyids to be subfamilies of the Echimyidae, based on the retention of the deciduous premolar in these taxa.

# Myocastor coypus (Molina, 1782)

Mus coypus Molina, 1782:287. Type locality "Rio Maipo, Santiago Province, Chile."

Myocastor coypus Kerr, 1792:225. First use of current name combination.

Myopotamus bonariensis Geoffroy St.-Hilaire, 1805:82. Type locality "Rio Parana, Paraguay."

Mastonotus popelairi Wesmael, 1841:61. Type locality "Bobica, Bolivia."

CONTEXT AND CONTENT. Context as noted in generic summary above. The species contains four subspecies (Willner, 1982):

M. c. bonariensis (Geoffroy St.-Hilaire, 1805:82), see above.

M. c. coypus (Molina, 1782:287), see above.

M. c. melanops (Osgood, 1943:132). Type locality "Quellón, Chiloe Island, Chile."

M. c. santacruzae (Hollister, 1914:57). Type locality "Rio Salado, Santa Cruz Province, Argentina."

**DIAGNOSIS.** Myocastor coypus (Fig. 1) is most similar to West Indian capromyid rodents (Woods, 1984). The deciduous premolars in both Myocastor and capromyids are retained throughout life; however in Myocastor the cheekteeth are extremely hypsodont and are always rooted (i.e., not hypselodont). Myocastor further differs in that the toothrows converge anteriorly and are inclined, and the upper cheekteeth markedly decrease in size anteriorly. The pattern of the upper re-entrant folds is modified from



Fig. 1. Photograph of a captive coypu (Myocastor coypus) from the zoo in Santiago, Chile. Photograph by L. Contreras.

two labial and two lingual folds that become lakes (fossettes) with wear. The incisors are broad, with orange-pigmented anterior surfaces. The skull is heavy with an elongated and anteriorly curved paraoccipital process. The angular process of the dentary is strongly deflected, and the coronoid process is vestigial (Fig. 2). The tail is long, terete, and scantily haired, and the hind feet are partially webbed.

GENERAL CHARACTERS. Myocastor coypus has a robust, highly arched body with short legs and a long, round tail (Fig. 1). The head is large and almost triangular, with a tapering muzzle, small ears, and long vibrissae. The mouth is valvular and the lips close behind the incisors to allow gnawing while submerged (Willner, 1982). The ears, eyes, and nostrils are located in the upper part of the head, reflecting the aquatic habits of the coypu (Mann, 1978).

Means and extremes (in parentheses) for external and cranial measurements (in mm) of adult non-captive *M. coypus* are: length of head and body, 521 (472-575); length of tail, 375 (340-405); length of hindfoot, 135 (120-150); length of ear, 27 (25-30); greatest length of skull, 114.2 (102.2-126.4); condylobasal length, 106.9 (94.0-117.4); zygomatic breadth, 68.1 (60.3-76.5); interorbital breadth, 31.1 (27.8-35.5); mastoid breadth, 50.9 (43.7-58.4); length of upper diastema, 32.1 (28.1-35.4); alveolar length of upper toothrow, 27.8 (22.5-29.3); length of mandibular symphysis, 34.5 (30.1-39.5); length of lower diastema, 20.2 (18.6-23.2); alveolar length of lower toothrow, 32.1 (30.5-33.3). Males (6.7 kg) generally are larger than females (6.36; Gosling, 1977).

The pelage consists of soft, dense underfur and long, coarse guard hairs (Mann, 1978). This underfur is densest on the abdomen and thickest during the winter months (Willner, 1982). Coloration ranges from yellow-brown to dark-brown (Chabreck and Dupuie, 1970; Nowak and Paradiso, 1983). The chin is covered by white hairs. The tail is scantily haired (Woods, 1984).

The first four digits of the hind feet are webbed; the fifth toe is free and used in grooming (Nowak and Paradiso, 1983). The front digits are strongly clawed, and the pollex is reduced. The soles of the feet are hairless (Woods, 1984).

DISTRIBUTION. Myocastor coypus is native to the Patagonian subregion (Fig. 3) of South America (Cabrera and Yepes, 1940; Mann, 1978). Two subspecies occur in Chile; M. c. coypus is widely distributed in the central zone and M. c. melanops is restricted to Chiloe Island (Mann, 1978; Osgood, 1943). M. c. santacruzae is found in Patagonia, M. c. bonariensis occurs in the northern part of Argentina, Bolivia, Paraguay, and souther Brazil



Fig. 2. Dorsal, ventral, and lateral views of cranium and lateral view of the lower jaw of the coypu (*Myocastor coypus*); University of Florida 9954, young adult male from Terrebonne Parish, Louisiana. Greatest length of cranium is 115 mm.

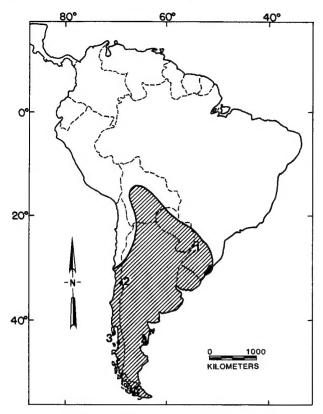


Fig. 3. The original natural range of the coypu (Myocastor coypus) in South America. Feral populations of the coypu are now established in many parts of the world. Type localities of subspecies are: 1, M. c. bonariensis; 2, M. c. coypus; 3, M. c. melanops; 4, M. c. santacruzae. Illustration by W. Zomlefer.

(Cabrera and Yepes, 1940), and M. c. popelairi is found in Bolivia (Osgood, 1943). As a result of escapes and liberations from fur farms, feral populations now occur in Europe, North America, northern Asia, Japan, East Africa, and the Middle East (Aliev, 1966a; Bar-Ilan and Marder, 1983; Corbet and Hill, 1980).

FOSSIL RECORD. Myocastorids presumably evolved in the Oligocene of South America from an echimyid of the subfamily Adelophomyinae. The family is first represented by *Prospaniomys* in the late Oligocene (Ameghino, 1902) and has remained an essentially Patagonian group since that time. Other fossil myocastorids are *Spaniomys* (Ameghino, 1887) from the early Miocene, *Haplostropha* and *Strophostephanus* (Ameghino, 1891) from the late Miocene, *Tribodon* (Ameghino, 1887) and *Proantherura* (Ameghino, 1906) from the early Pliocene, and *Paramyocastor* (Ameghino, 1904) and *Isomyopotamus* (Rovereto, 1914) from the late Pliocene. *Graphiomys* is considered a synonym of *Spaniomys* by Patterson and Pascual (1968). *Neoreomys*, often classified with *Myocastor* and the capromyids, is considered a dasyproctid by Wood and Patterson (1959).

FORM. Myocastor c. melanops of southern Chile is darker than M. c. coypus from central Chile (Housse, 1953; Osgood, 1943). The darker coloration in M. c. melanops may be related to cooler temperatures and higher humidity in southern Chile (Mann, 1978).

The female has four or five pairs of mammae located dorsolaterally (Dobson and De Viney, 1967; Gosling, 1980). The position of the mammae may be an adaptation for suckling young while swimming (Newson, 1966) and allows the coypu to sit in an alert posture while nursing young on the nest (Weir, 1974). The mammary glands are approximately circular in dorsal aspect. The color and extent of development of the mammae depends upon the reproductive stage; the external suctorial apparatus is a true nipple with three main ducts (Dobson and De Viney, 1967; Gosling, 1980).

An oily secretion from glands located at the base of sensory bristles near the mouth and anus lubricates the pelage as the coypu grooms itself, and secretions from this gland are used to delineate the home range (Ehrlich, 1958). The mean mass of the anal gland is greater in males (12.2 g) than females (4.1 g; Gosling, 1977).

The skull is heavy with a large sagittal crest and a broad infraorbital foramen that lacks a groove for nerve passage. The internal carotid and stapedial arterial stems are both lacking. The lateral process of the squamosal is distinct. The zygomatic arch is broad with a thick jugal bone and a small jugal fossa. The jugal is not in contact with the lacrimal bone and the lacrimal canal does not open on the side of the rostrum (Woods, 1984; Woods and Howland, 1979).

Myocastor chews obliquely, unilaterally, and has many plagiognathus adaptations (Woods, 1976; Woods and Howland, 1979). The bones and musculature of the posterior legs are well developed. The pelvis possesses a long iliac bone. The femur has a well-developed trochanter for attachment of the muscles involved in swimming, and a well-developed deltoid crest and large subscapular fossa aid in burrowing (Mann, 1978). The cutaneous maximus muscle is massive and similar in form to that of most other hystricognath rodents (Woods and Howland, 1977). The left adrenal gland is kidney shaped and larger than the hooked-shaped right adrenal gland (Wilson and Dewees, 1962; Wilson et al., 1964). The ratio of adrenal mass to body mass is greater in the adult coypu than in other mammals, and the glands are mainly composed of cortical tissue (Katomski and Ferrante, 1974). The caecum is large (Martin, 1835); the colic caecum is closed (Wagner, 1963).

The penis points posteriorly, as in most hystricognath rodents (Contreras and Bostos-Obregon, 1980; Weir, 1974). It consists of a prepuce and a glans penis that contains the saccullus urethralis and baculum. The baculum is cylindrical and composed of an ossified bone, a transition zone, and a cartilaginous tip. Bacular length ranges from 15 to 23 mm, and diameter from 1 to 4 mm. The surface of the glans is covered by minute scales and there are no large spicules at the bottom of the sacullus urethralis (Hillemann et al., 1958; Pocock, 1922; Spotorno, 1979). There are three accessory sex glands: coagulating, seminal vesicular, and bulbourethral (Mann and Wilson, 1962). The secretions of these glands cause the seminal fluid to gel and form a copulatory plug. At the age of 4-5 months the male becomes sexually active and ketosteroid hormone and cholesterol content increases in the testes and adrenal cortex (Pietrzyk-Walknowska, 1956). The testes descend from the abdominal cavity to the inguinal cavity at sexual maturity (Peloquin, 1969). Mean testis mass in adults is about 4.8 g (Brown, 1975).

The vaginal orifice lies below a prominent urinary papilla. A cartilaginous os clitoris is present. The uterus is duplex, and the ovaries are not encapsulated. Ovaries attain an average length, diameter, and mass of 12 mm, 7.5 mm, and 186 mg, respectively (Hillemann et al., 1958). The vaginal orifice opens in the 4th or 5th month (Peloquin, 1969); it has been reported to never close (Atwood, 1950; Weir, 1974), to close to some extent (Peloquin, 1969), or to completely close (Gosling et al., 1981). The placenta has a well-developed decidua basalis connected to the uterine wall by large blood vessels (Newson, 1966).

FUNCTION. Coypus are nocturnal; the interval between the end of the active period and sunrise is inversely related to temperature (Gosling, 1979). Most of the active period is spent feeding, grooming, and swimming. Chabreck (1962) also found that coypus mainly were nocturnal, but found no relationship between activity and temperature. During cold nights, coypus spend the pre-dawn hours huddling together (Gosling, 1979), perhaps to conserve energy (Contreras, 1984). They become diurnal during cold periods to recover feeding time lost while huddling at night (Gosling et al., 1980a). In captivity, animals primarily are nocturnal, although they become conditioned to diurnal activity when fed during the day (Lomnicki, 1957).

Body temperature of coypus is labile, and correlates positively with air temperature. During the summer, coypus in Cuba have an average basal metabolic rate of 0.692 cc O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (Segal, 1978). This value is 164% of that expected based on Kleiber's (1961) relationship of basal metabolic rate and body mass. The vascular supply to the tail and distal parts of the limbs is used in thermoregulation. Coypus also have an extremely high thermal conductance (Segal, 1978). When the air temperature is 0°C, body temperature may drop to 33°C. Newborn coypus can control their body temperature over a wide ambient range (Hull, 1973).

Coypus can remain submerged for >10 min (Katomski and Ferrante, 1974). During a dive, there is a decrease in the left

ventricular contractibility mediated by cholinergic and andrenergic influences (Ferrante and Opdyke, 1969). Bradycardia increases oxygen conservation during the first minute of submergence, before peripheral vasoconstriction reaches maximum values (Ferrante, 1970). Some cardiovascular responses of the coypu during diving are obtainable, in part, independent of intrathoracic pressure changes and response of receptors in the nares to water (Ferrante and Frankel, 1971). Determinations of blood gases and pH after a 5-min submersion indicate respiratory insensitivity to the combined effects of hypoxia, hypercapnia, and acidosis (Ferrante and Miller, 1971). High whole body buffer values indicate that the coypu is equipped with physiological mechanisms that effectively regulate pH during hypercapnia. These mechanisms are not present in the blood itself, because the blood buffer value is similar to values for other surfacedwelling mammals (Bar-Ilan and Marder, 1983). The coypu possesses a vascular neuro-effector system organized to greatly restrict the blood supply to skeletal muscle, kidney, and intestine during a dive (Folkow et al., 1971). This distributes available oxygen reserves preferentially to the brain and myocardium. Coypus have a low red blood cell count (3.4  $\times$  10<sup>-6</sup>/ml), but the red blood cells are unusually large; leucocyte levels are 8,300/ml (Scheuring and Bratkowska, 1976).

In certain diving mammals, the ratio of adrenal mass to body mass is greater than in terrestrial mammals (Slipjer, 1958, 1962) and norepinephrine far exceeds epinephrine (West, 1955). Though the coypus has the largest relative adrenal mass of any mammal studied, epinephrine values exceed norepinephrine and are similar to other rodents (Katomski and Ferrante, 1974). An adrenal index has been used to indirectly measure the stress to which coypus from natural populations have been exposed (Willner et al., 1979).

The acoustic and tactile senses are well developed. There is a large inferior culliculus and the pinnae are large for an aquatic animal. The large peribuccal vibrissae and the extraordinary development of the trigeminal nerve indicate the importance of mechanoreception (Mann, 1978).

Coypus feed and defecate throughout their active period; up to 86% of their feces are produced in the water. Coprophagy occurs when the animals return to the nest (Gosling, 1979). Fecal pellets are approximately 5 cm long, oblong in shape, with fine longitudinal grooves (Willner, 1982).

ONTOGENY AND REPRODUCTION. The age of embryos can be estimated from their fetal mass or crown to rump length (Chapman et al., 1980; Newson, 1966). Embryonic development is slow for the first month of gestation, while the embryo is embedded in a tissue mass formed at each implantation site (Newson, 1965, 1966).

The potential longevity of M. coypus is  $6.3 \pm 0.4$  years. As in other hystricognathous rodents from South America, the coypu has a longer gestation period than would be predicted by body mass (Blueweiss et al., 1978; Kleiman et al., 1979; Sacher and Staffeldt, 1974). Gestation period varies from 127 to 139 days (Atwood, 1950; Cabrera and Yepes, 1940; Newson, 1966; Skowron-Cendrzak, 1956; Weir, 1974). The age of first parturition is variable, ranging from 6 to 15 months (Gosling, 1974; Konieczna, 1956). Cholesterol and ketosteroid levels increase as ovaries of young females develop. Large amounts of these substances are found in the ovary and adrenal cortex during estrus; in contrast, only small amounts are found in pregnant females (Konieczna, 1956). The coypu is polyestrus (Skowron-Cendrzak, 1956). The length of the estrus cycle is variable; intervals may range from 5 to 60 days, with healthy females showing no cycles over several months (Newson, 1966; Wilson and Dewees, 1962). This variation suggests that ovulation is coitus-induced (Asdell, 1964). The estrus condition seldom exceeds 2 days (Skowron-Cendrzak, 1956). There is a post-partum estrus within 2 days of parturition (Gosling, 1981a; Matthias, 1941). The mean post-partum interval is about 2.1 weeks (Gosling, 1981a).

Coypus are nonseasonal breeders (Brown, 1975; Gosling et al., 1980b; Kim, 1980; Willner et al., 1979). Peak birth periods occur in January, March, May, and October in Oregon (Peloquin, 1969), and December-January and June-July in Louisiana (Adams, 1956). Mean litter size generally is from three to six (range, 1-12; Federspiel, 1941; Gosling, 1981b). Litter size declines during the winter months (Gosling and Baker, 1981; Gosling, 1981b; Newson, 1966; Willner et al., 1979), and is larger in areas where food is abundant and winters are mild (Brown, 1975). More fetuses are found in the right than the left uterine horn (Adams, 1956; Rowlands and Heap,

1966; Willner et al., 1979). Mean number of corpora lutea is approximately eight (ranges, 3-17; Gluchowski and Maciejowski, 1958; Peloquin, 1969; Rowlands and Heap, 1966). There are more corpora lutea than embryos and they have a tendency to progressively decrease in number. The coypu may be polyovular (Gluchowski and Maciejowski, 1958).

The annual productivity for a population of coypus in Maryland is 8.1 young/female (Willner et al., 1979). Factors affecting reproductive potential of coypus are food type and availability, weather conditions, predators, and disease (Evans, 1970). Where environmental conditions are not limiting, adult females have 2.7 litters/year and produce an average of 15 young/year (Brown, 1975).

About 26–28% of litters are aborted (Newson, 1966). Partial abortion also has been detected (Gluckowski and Maciejowski, 1958). Coypus will selectively abort small, predominantly-female litters (Gosling, 1986), which may be a mechanism for controlling the quality and sex of offspring. If an embryo dies in an early stage of development, the junction between the placental disc and the decidua basalis breaks, leaving the embryo and placental disc to resorb. The decidua atrophies and becomes necrotic, but persists until parturition (Newson, 1966). The embryo may become mummified following death. Reabsorption rates range from 6 to 24.6%, and seem to be greater during inclement weather and with habitat deterioration (Atwood, 1950; Newson, 1966; Peloquin, 1969; Willner et al., 1979).

The young are precocial. Mean body mass at birth is about 225 g (Newson, 1966) and they rapidly gain weight during the first 5 months (Peloquin, 1969). Daily growth rates for males and females were 0.0116 g/day and 0.0120 g/day, respectively. Low temperatures slow growth rates (Dixon et al., 1979). There is no difference in mass between males and females at birth, however, fully grown males are up to 15% heavier than females (Doncaster and Micol, 1989). The young are covered by soft-down hair; the tail hairs appear silky until the end of the 1st month when coarse hairs develop. Lactation in feral coypus in England is estimated to occur at 7.7 weeks (Gosling, 1980). In captivity, young are nursed for 2 months, but can survive if weaned at 5 days (Newson, 1966). Milk of coypus contains 41.5% dry matter, 27.9% fat, 13.7% protein, 0.5% sugar, and 1.3% ash (Ehrlich, 1958).

Molar wear and eruption rates have been used to determine age in captive coypus (Aliev, 1965b, 1965c, 1965d). Body mass has been used to age feral coypus up to 6 years for males and 2 years for females (Willner et al., 1980). Age also can be estimated based on eye-lens mass. Variables such as sex and nutritional status have a negligible effect on lens mass (Gosling et al., 1980b). Brown (1975) classified coypu as juveniles, subadults, and adults based on body mass and pelage characteristics. Adams (1956) classified them in a similar way, but used length of hind foot.

**ECOLOGY.** Coypus live in a variety of aquatic habitats. Their habitat in Chile is waterways, rivers, lakes, and marshes, especially in areas with emergent vegetation or succulent vegetation along the banks. They are chiefly lowland animals, but may range up to 1,190 m in the Andes (Greer, 1966).

Feral coypus generally construct burrows in banks with 45–90° slopes (Peloquin, 1969). Burrows can extend from 1 to 6 m and have several entrances (Atwood, 1950; de Soriano, 1960; Laurie, 1946; Peloquin, 1969). In Argentina, burrow temperature was 8–10°C, while ambient temperature ranged from –4 to 24°C (de Soriano, 1960). Platform nests are constructed of local vegetation (Willner, 1982).

Damage by coypus is minimal, except at high densities (Ehrlich and Jedynak, 1962; Ellis, 1963; Harris and Webert, 1962; Hillbricht and Ryszkowski, 1961; Litjens, 1980; Wentz, 1971). However, they are known to disrupt drainage systems, damage crops, and disturb natural plant communities. Burrows sometimes penetrate or weaken the river banks that keep low-lying areas of drained agricultural land from flooding (Cotton, 1963). In California, 11% of the area along edges of sugarcane fields was damaged. Coypu may feed upon alfalfa, rice, ryegrass (Schitoskey et al., 1972), and seedlings of bald cypress (Blair and Langlinais, 1960). They may damage fruit and nut trees, conifers, and deciduous forest trees (Kuhn and Peloquin, 1974). In England, they feed on almost every available crop, but selective feeding on cowbane (Circuta virosa) and great water dock (Rumex hydrolapathum) has been documented (Ellis, 1963, 1965). Root crops are mainly eaten in the winter (Ellis, 1963; Gosling, 1974).

At high densities, coypus can reduce the numbers of emergent plants, forming areas of open water (Ellis, 1963, 1965; Wentz, 1971). This kind of impact on aquatic vegetation may have led to some introductions of coypus based on rumors that they would eat undesirable aquatic plants. This would cause some investigators to argue that the coypu is a biocontrol mistake, however, Conner (1989) argues that the coypu originally was introduced into Louisiana for its fur potential. The original introductions into Louisiana, like so many other places, probably were via a variety of sources such as escaped captive breeding operations, private landowners, and official projects. In Louisiana, these introductions mainly occurred in the late 1930s and early 1940s. They multiplied rapidly in the 1940-1950s, and by 1959 there were over 20,000,000 coypu in Louisiana (Lowery, 1974). The first pelts reached the fur market in 1943-1944, and the harvesting of coypus grew to the point that nearly 1,000,000 pelts were harvested during the 1986-1987 trapping season (Conner, 1989).

Examples of damage by coypus at high densities in Louisiana, include the destruction of baldcypress and *Spartina alterniflora* seedlings almost as fast as they were planted, and the interruption of successional patterns in freshwater marshes. In Louisiana wetlands, the coypu may be the dominant force in destroying desirable vegetation and preventing revegetation in swamp forests and marshes (Conner, 1989).

Evans et al. (1971) compared different trapping, handling, and marking methods. Victor #2 and #1½ are more effective in catching coypus than Conibear 220. The Conibear is effective in killing the animal (Linscombe, 1976; Palmisano and Dupuie, 1975). Survival rates are higher for live-trapped animals than for leg-hold trapped animals (Chapman et al., 1978). Attempts to mark coypus with pressurized refrigerant have not been successful (Lazarns and Rowe, 1975; Lopetegui, 1980).

Control procedures include trapping, chemical control, baiting, and shooting (Kuhn and Peloquin, 1974; Schitoskey et al., 1972; Talbert, 1962). Necropsies on animals given the rodenticide prolin revealed that the lips turned yellow-green, massive hematoma was present in the thoracic region, and bleeding occurred from the penis, nostrils, and lips (Kuhn and Peloquin, 1974). Modification of farming practices can minimize the damage caused by coypus (Evans, 1970). In Chile, dogs have been used to track and kill coypus in agricultural areas (Greer, 1966).

Food consumption by coypus in Chile fluctuates between 700 and 1,500 g (average, 1,100 g) of green mater in 24 h (Christen, 1978), approximately 25% of their body mass (Gosling, 1974). The coypu is an opportunistic feeder, consuming a great variety of plants throughout its natural and introduced range. The diet consists largely of aquatic vegetation: stems, leaves, roots, and even bark (Murua et al., 1981; Warkentin, 1968). Coypus may use logs or other floating objects as feeding platforms (Atwood, 1950). Similar food habits have been found for the coypu and the muskrat (Ondatra zibethica) throughout the year in Maryland; thus there may be competition for food resources between these animals. In contrast with muskrats, algae is not an important component of the diet of the coypu (Willner et al., 1979).

Estimates of population density range from 0.1 (Valentine et al., 1972) to 25/ha (Brown, 1975; Greer, 1966). Doncaster and Micol (1989) indicated that coypus do not occupy all of the available habitat and, in their study, 40% of suitable habitat was unoccupied in late winter in France. They, therefore, measured population densities as patch densities (density in occupied habitat). Their patch densities for coypus in France ranged from 2.42/ha in May to 9.14/ha in November. Density is dependent upon habitat type, pollution, and weather (Brown, 1975; Willner et al., 1979), but is not dependent on food availability (Doncaster and Micol, 1989). A nutrientrich cattle sewage lagoon in Florida had a density considerably greater than a nearby unpolluted pond (24.7 versus 5.9/ha; Brown, 1975). Estimates of densities in a Louisiana refuge fluctuated between 0.10 and 1.29/ha from 1960 to 1965 (Valentine et al., 1972).

Home range is fairly constant in spite of population density. The average home range for female coppus in France was 2.47 ha, while for males it was 5.68 ha (Doncaster and Micol, 1989).

Population numbers may be greatly reduced by severe cold weather (Doncaster and Micol, 1989). Cold weather reduces fat reserves and stimulates abortion, leading to reproductive failure and adult mortality (Newson, 1966; Norris, 1967). The sensitivity of coypus to climatic conditions may be the most important factor in determining population size (Doncaster and Micol, 1989). Coypu

populations expand rapidly during mild winters; thermal pollution increases the chances of survival during cold weather (Litjens, 1980).

Generally, coypus remain in one area throughout their life; however, freezing weather or drought may cause migration (Aliev, 1968). The daily cruising range is <45 m (Adams, 1956). Fifty percent of tagged males were recaptured within 91.4 m (Kays, 1956); 80% within 0.4 km, and 20% between 0.4 and 1.25 km (Robicheaux, 1978). In the Netherlands, feeding coypus may travel as far as 300 m through the water and 50 m on the bank (Kim, 1980). The longest recorded distance traveled in brackish water is 3.2 km (Linscombe et al., 1981), though they have been reported to disperse 120 km downstream over a 2-year period (Aliev, 1968). The best method of radiocollar telemetry consists of a nylon-covered rubber-tubing collar with a 60-g transmitter 14% larger than the circumference of the neck (Coreil and Perry, 1977).

Estimates of mortality rates (including natural as well as trapping mortality) range from 53 (Chapman et al., 1978) to 74%annually (Newson, 1969). Coypus can be infected by toxoplasmosis (Holmes et al., 1977), pappilomatosis (Jelinek et al., 1978), rabies (Matouch et al., 1978), equine encephalomyelitis (Page et al., 1957), salmonellosis (Safarov and Kurbanova, 1976), paratyphoid (Evans, 1970), leptospirosis (Twigg, 1973), richettsia (Kovalev et al., 1978), sarcoporidiosis (Scheuring and Madej, 1976), and coccidiosis (Michalski and Scheuring, 1979). Coccidiosis, which causes creeping eruption in human skin, may reduce fecundity and also may be fatal to coypus (Evans, 1970). Endoparasites include 11 trematodes, 21 cestodes, and 31 nematodes (Babero and Lee, 1961), with the most important ones in South America being the nematodes Graphidioides myocastoris, Trichuris myocastoris, and Dipetalonema travassoso, the trematode Hippocrepis myocastoris, and the cestode Rodontolepis sp. (Babero et al., 1979). Important ectoparasites are biting lice (Pitrufquenia coypus), fleas (Ceratophyllus gallinae), and ticks (Ixodes ricinus, I. arvicolae, I. hexagonus, I. trianguliceps, Dermacentor variabilis; Newson and Holmes, 1968; Willner, 1982).

Coypus are taken by a wide variety of predators. Aliev (1966a) reports that domestic dogs (Canis familiaris), golden jackals (C. aureus), gray wolves (C. lupus), and the jungle cat (Felis chaus) are the most important mammalian predators on the coypus in the Soviet Union. In South America, the most important mammalian predators are the jaguar (Felis onca), mountain lion (F. concolor), ocelot (F. pardalis), and little spotted cat (F. tigrinus; Dennler, 1930). Other mammals reported to feed on coypus are Canis rufus, Vulpes vulpes, and Mustela erminea (Willner, 1982). Birds of prey such as the red-shouldered hawk (Buteo lineatus), marsh harrier (Circus aeruginosus), and the tawny owl (Strix aluco) also take large numbers of coypus (Aliev, 1966b; Ellis, 1965; Warkentin, 1968). Aliev (1966b) considers caymans (Caiman longirostris, C. sclerops, and C. niger) to be the most serious enemies of coypus in South America. Wolfe et al. (1987) studied the food habits of the American alligator (Alligator mississippiensis) in Louisiana, and found that coypus represented 59.6% of their diet by weight. Young coypus also are preyed upon by gar (Lepisosteus), turtles, and large snakes (Agkistrodon picivorous) (Evans, 1970; Warkentin, 1968).

Female coypus can delay parturition for up to 3 days if they are disturbed, which may be adaptive in allowing them to avoid detection by predators and improve the chances of survival of their young (Gosling et al., 1988). Females also may avoid detection by predators by isolating themselves in dense vegetation before giving birth (Gosling et al., 1984). Coypus usually have their litters in open nests at the edge of a body of water, or in large nest chambers located deep in their burrows (Gosling et al., 1988).

BEHAVIOR. Most of the active period is spent feeding, grooming, and swimming. Forepaws are used to hold and manipulate food. The coypu grooms by scratching and by nibbling movements of the mouth. They swim using alternate propulsive thrusts of webbed hind feet and sometimes float immobile on the water surface (Gosling, 1979)

Coypus are highly gregarious (Ehrlich, 1966; Gosling, 1977; Warkentin, 1968). Ryskowski (1966) studied animals crowded in captivity and concluded that adults were solitary. Groups usually consist of 2–13 animals, and are composed of related adult females, their offspring, and a large male. Young adult males are expelled and occasionally found solitary (Gosling, 1977; Warkentin, 1968). Warkentin (1968) identified an alpha male and female. Females are dominant over males except during mating (Warkentin, 1968). Males

vigorously defend the nest area after a new litter is produced (Carill-Worsley, 1932; Ehrlich, 1966; Ryszkowski, 1960).

Daytime activity in Louisiana is influenced by temperature. Sunning and sleeping are the main activities at temperatures <28°C; at higher temperatures most animals fed, groomed, or slept. No animals were found sunning above 34°C (Warkentin, 1968).

GENETICS. The diploid number of chromosomes is 42, with 7 pairs of metacentric, 10 pairs of submetacentric, and 4 pairs of telocentric chromosomes (George and Weir, 1974; Tsigalidou et al., 1966). The fundamental number is 76. The karyotype is represented by dibrachial chromosomes; the Y chromosome is small and acrocentric. One pair of chromosomes carries satellites (Kasumova et al., 1976).

Blood groups include two types of antibodies (CO 1 and CO 2; Szynkiewicz, 1968). Coypu from six breeding centers in Poland showed different gene frequencies of beta-globulin (Szynkiewicz, 1971). Adults possess an additional serum protein. The concentration of globulins and albumin is greater in adults, and there is a difference in lipoprotein between fetuses and adults (Brown, 1966).

Analysis of serum proteins, lens proteins, and liver enzymes indicated that a population in Maryland was genetically homogeneous. All analyzed serum protein systems were monomorphic and characterized by the typical mammalian albumin and transferrin (Morgan et al., 1981).

REMARKS. Myocastor c. popelairi (Wesmael, 1841) is synonymized with M. c. coypus because the type specimen came from Chile, not Bobica, Bolivia, and the distinguishing character (the nipples located high on the back) is considered an individual anomaly. The higher-level classification of the coypu is unresolved. Though myocastorids are related to echimyids and capromyids, there are too many morphological differences to unite myocastorids with either of these taxa in the same family (Woods, 1972, 1982; Woods and Howland, 1979).

Although the common name for this species in English-speaking countries frequently is nutria, this name in Spanish refers to an otter. Therefore, the best common name is the one widely used in Latin America, coypu.

### LITERATURE CITED

- ADAMS, W. H., JR. 1956. The nutria in coastal Louisiana. Proceedings of the Louisiana Academy of Sciences, 19:28-41.
- ALIEV, F. F. 1965a. Extent and causes of nutria mortality in the water bodies of the southern USSR. Mammalia, 29:435-437.
- ——. 1965b. Growth and develoment of nutrias' functional features. Fur Trade Journal of Canada, 42(11):2-3.
- ——. 1965c. Growth and development of nutrias' functional features. Fur Trade Journal of Canada, 42(12):2-3.
- -----. 1965d. Growth and development of nutrias' functional features. Fur Trade Journal of Canada, 43(2):2-3.
- -----. 1966a. Numerical changes and the population structure of the coypu (*Myocastor coypus*, Molina) in different countries. Saugetierkundliche Mitteilungen, 15:238-242.
- ——. 1966b. Enemies and competitors of the nutria in USSR. Journal of Mammalogy, 47:353-355.
- ——. 1968. Contribution to the study of nutria-migrations, Myocastor coypus (Molina, 1782). Saugetierkundliche Mitteilungen, 16:301-303.
- AMECHINO, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia. Boletín del Museo la Plata (Buenos Aires), 1:1-26.
- ——. 1891. Nuevos restos de mamíferos fósiles, descubiertos por C. Ameghino en el eoceno inferior de la Patagonia Austral. Revista Argentina de Historia Natural, 1:289-328.
- ——. 1904. Nuevas especies de mamíferos. Cretaceos y Terciarios de la República Argentina. Anales de la Sociedad Científica Argentina, 56-58:1-142.
- 1906. Les formations sédimentaires du Crétacé Supérieur et du Tertiaire de Patagonie. Anales del Museo Nacional de Historia Natural de Buenos Aires, 15:1-568.
- ASDELL, S. A. 1964. Patterns of mammalian reproduction. Second

- edition. Comstock Publishing Associates, Ithaca, New York, 670 pp.
- ATWOOD, É. L. 1950. Life history studies of nutria, or coypu, in coastal Louisiana. The Journal of Wildlife Management, 14: 249-265.
- Babero, B. B., and J. W. Lee. 1961. Studies on the helminths of nutria, *Myocastor coypus* (Molina), in Louisiana with check list of other worm parasites from this host. The Journal of Parasitology, 47:378-390.
- BABERO, B. B., C. CABELLO, AND J. KINOED. 1979. Helmintofauna de Chile. Part 5. Nuevos Parasitos del Coipo *Myocastor coypus* (Molina, 1782). Boletín de Parasitologia de Chile, 34:26–31.
- BAR-ILAN, A., AND J. MARDER. 1983. Adaptations to hypercapnic conditions in the nutria (Myocastor coypus)—in vivo and in vitro CO<sub>2</sub> titration curves. Comparative Biochemistry and Physiology, 75A:603-608.
- BLAIR, R. M., AND M. J. LANGLINAIS. 1960. Nutria and swamp rabbits damage baldcypress plantings. Journal of Forestry, 58: 388-389.
- Blueweiss, L., et al. 1978. Relationships between body size and some life history parameters. Oecologia (Berlin), 37:257-272.
- Brown, L. E. 1966. An electrophoretic comparison of the serum proteins of fetal and adult nutria (*Myocastor coypus*). Comparative Biochemistry and Physiology, 19A:479-481.
- Brown, L. N. 1975. Ecological relationships and breeding biology of the nutria (*Myocastor coypus*) in the Tampa, Florida, area. Journal of Mammalogy, 56:928-930.
- CABRERA, A., AND J. YEPES. 1940. Mamiferos Sud-Americanos (vida, costumbres y descripcion). Compania Argentina de Editores, Buenos Aires, 370 pp.
- CARILL-WORSLEY, P. E. T. 1932. A fur farm in Norfolk. Transactions of the Norfolk and Norwich Naturalists' Society, 13: 105-115.
- Chabreck, R. H. 1962. Daily activity of nutria in Louisiana. Journal of Mammalogy, 43:337-344.
- CHABRECK, R. H., AND H. H. DUPUIE. 1970. Monthly variation in nutria pelt quality. Proceedings of the Southeastern Association of Game and Fish Commissioners, 24:169-175.
- CHAPMAN, J. A., G. R. WILLNER, K. R. DIXON, AND D. PURSLEY. 1978. Differential survival rates among leg-trapped and livetrapped nutria. The Journal of Wildlife Management, 42:926– 928.
- CHAPMAN, J. A., J. C. LANNING, G. R. WILLNER, AND D. PURSLEY. 1980. Embryonic development and resorption in feral nutria (Myocastor coypus) from Maryland. Mammalia, 44:371-379.
- CHRISTEN, M. F. 1978. Evaluación nutritiva de cuatro dietas monoespecificas en la alimentación del coipo (Myocastor coypus Molina 1782). Tesis Faculitad de Medicina Veterinaria, Universidad Austral de Chile, Valdivia.
- CONNER, W. H. 1989. The nutria problem—part III: reply to rebuttal. Aquaphyte, 9:14.
- CONTRERAS, L. C. 1984. Bioenergetics of huddling: test of a psycho-physiological hypothesis. Journal of Mammalogy, 65: 256-262.
- CONTRERAS, L. C., AND E. BOSTOS-OBRECON. 1980. The anatomy of the reproductive tract in *Octodon degus*: a non-scrotal rodent. Archives of Andrology, 4:115-124.
- CORBET, G. B., AND J. E. HILL. 1980. A world list of mammalian species. British Museum (Natural History), London, 226 pp.
- COREIL, P. D., AND H. R. PERRY, JR. 1977. A collar for attaching radio transmitter to nutria. Proceedings of the Southeastern Association of Game and Fish Commissioners, 31:254-258.
- COTTON, K. E. 1963. The coypu. The Rivers Boards Association Year Book, 11:31-39.
- DE SORIANO, B. S. 1960. Elementos constitutivos de una habitación de *Myocastor coypus bonariensis* (Geoffrey) ("nutria"). Revista de la Facultad de Humanidadas y Ciencias serie Ciencias Biológicas, 18:257–276.
- Dennler, G. 1930. Die Nutria in ihrer Hiemat. Der Deutsch Pelztierzuchter, 2:4-45.
- DIXON, K. R., G. R. WILLNER, J. A. CHAPMEN, W. C. LANE, AND D. PURSLEY. 1979. Effects of trapping and weather on body weights of feral nutria in Maryland. Journal of Applied Ecology, 16:69-76.
- Dobson, W. J., and G. T. De Viney. 1967. The mammary systems of the nutria *Myocastor coypus*. BioScience, 17:905.
- DONCASTER, C. P. AND T. MICOL. 1989. Annual cycle of a coypu

- (Myocastor coypus) population: male and female strategies. Journal of Zoology (London), 217:227-240.
- EHRLICH, S. 1958. The biology of the nutria. Bamidgeh, 10:36-43, 60-70.
- —. 1966. Ecological aspects of reproduction in nutria Myocastor cospus Molina. Mammalia, 30:142-152.
- EHRLICH, S., AND K. JEDYNAK. 1962. Nutria influence on a bog lake in northern Pomorze, Poland. Hydrogiologia, 19:273-
- ELLIS, E. A. 1963. Some effects of selective feeding by the coypu (Myocastor coypus) on the vegetation of Broadland. Transactions of the Norfolk and Norwich Naturalists' Society, 20: 32-35.
- 1965. The Broads. Collins, London, 401 pp.
- Evans, J. 1970. About nutria and their control. United States Bureau of Sport Fisheries and Wildlife, Resource Publication, 86:1-65.
- Evans, J., J. O. Ellis, R. D. Nass, and A. L. Ward. 1971. Techniques for capturing, handling, and marking nutria. Proceedings of the Southeastern Association of Game and Fish Commissioners, 25:295-315.
- FEDERSPIEL, M. N. 1941. Nutria farming. American Fur Breeder, 13:12-13.
- FERRANTE, F. L. 1970. Oxygen conservation during submergence apnea in a diving mammal, the nutria. American Journal of Physiology, 218:363-371.
- FERRANTE, F. L., AND H. M. FRANKEL. 1971. Cardiovascular responses of anesthetized nutria and cats during apnea. American Journal of Physiology, 221:251-254.
- FERRANTE, F. L., AND B. D. MILLER. 1971. Respiratory insensitivity to blood gases in nutrias (Myocastor coypus). Journal of Applied Physiology, 31:175-177.
  FERRANTE, F. L., AND D. F. OPDYKE. 1969. Mammalian ventric-
- ular function during submersion asphyxia. Journal of Applied Physiology, 26:561-570.
- FOLKOW, B., B. LISANDER, AND B. OBERG. 1971. Aspects of the cardiovascular nervous control in a mammalian diver (Myocastor coypus). Acta Physiologica Scandinavica, 82:439-
- Geoffroy St.-Hilaire, E. 1805. Mémoire sur un nouveau genre de mammifères nommé Hydromys. Annales de Musée National d'Historie Naturelle, Paris, 6:81-90. GEORGE, W., AND B. J. WEIR. 1974. Hystricomorph chromo-
- somes. Symposia of the Zoological Society of London, 34:79-
- GLUCHOWSKI, W., AND J. MACIEJOWSKI. 1958. Investigation on factors controlling fertility in the coypu. II. Attempts at determining potential fertility based on histological studies of the ovary. Annales Universitatis Mariae Curie-Sklodowska Sectio E Agricultura, 13:345-361.
- Gosling, L. M. 1974. The coypu in East Anglia. Transactions of the Norfolk and Norwich Naturalists' Society, 23:49-59.
- —. 1977. Coypu. Pp. 256-265, in The handbook of British mammals. Second edition (G. B. Corbet and H. N. Southern, eds.). Blackwell Scientific Press, Oxford, 520 pp.
- -. 1979. The twenty-four hour activty cycle of captive coypus Myocastor coypus. Journal of Zoology (London), 187: 341 - 367.
- 1980. The duration of lactation in feral coypus, (Myocastor coypus). Journal of Zoology (London), 191:461-474.
- 1981a. The dynamics and control of a feral coypu population. Pp. 1806-1825, in Proceedings of the worldwide furbearer conference (J. A. Chapman and D. Pursley, eds.). Worldwide Furbearer Conference Inc., Frostburg, Maryland, 3:1553-2056.
- . 1981b. Climatic determinants of spring littering by feral coypus, Myocastor coypus. Journal of Zoology (London), 195: 281-288.
- 1986. Selective abortion of entire litters in the coypu (Myocastor coypus): adaptive control of offspring production in relation to quality and sex. American Naturalist, 127:772-
- Gosling, L. M., and S. J. Baker. 1981. Coypu (Myocastor coypus) potential longevity. Journal of Zoology (London), 197:
- GOSLING, L. M., S. J. BAKER, AND K. M. H. WRIGHT. 1984. Differential investment by female coypus (Myocastor coypus)

- during lactation. Symposia of the Zoological Society of London, 51:273-300.
- Gosling, L. M., G. E. Guyon, and K. M. H. Wright. 1980a. Diurnal activity of feral coypus (Myocastor coypus) during the cold winter of 1978-9. Journal of Zoology (London), 192: 143-146.
- Gosling, L. M., L. W. Huson, and G. C. Addison. 1980b. Age estimation of coypus (Myocastor coypus) from eye lens weight. Journal of Applied Ecology, 17:641-648.
- GOSLING, L. M., A. D. WATT, AND S. J. BAKER. 1981. Continuous retrospective census of the East Anglian coypu population between 1970 and 1979. Journal of Animal Ecology, 50:885-901.
- Gosling, L. M., K. M. H. Wright, and G. D. Few. 1988. Facultative variation in the timing of parturition by female coypus (Myocastor coypus), and the cost of delay. Journal of Zoology (London), 214:407-415.
- GREER, J. K. 1966. Mammals of Malleco Province Chile. Publications of the Museum, Michigan State University Biological Series, 3:49-152.
- HALL, E. R. 1981. The mammals of North America. Second edition. John Wiley and Sons, New York, 2:601-1181 + 90.
- HARRIS, V. T., AND F. WEBERT. 1962. Nutria feeding activity and its effect on marsh vegetation in southwestern Louisiana. United States Fish and Wildlife Service, Special Scientific Re-
- HILLBRICHT, A., AND L. RYSZKOWSKI. 1961. Investigations of the utilization and destruction of its habitat by a population of coypu, Myocastor coypu Molina, bred in semi-captivity. Ekologia Polska, seria A, 9:506-524.
- HILLEMANN, H. H., A. I. GAYNOR, AND H. P. STANLEY. 1958. The genital systems of nutria (Myocastor coypus). Anatomical Record, 130:515-531.
- HOLMES, R. G., O. ILLMAN, AND J. K. A. BEVERLEY. 1977. Toxoplasmosis in coypu. Veterinary Record, 101:74-75.
  HOLLISTER, N. 1914. Four new neotropical rodents. Proceedings
- of the Biological Society of Washington, 27:57-59.
- Housse, P. R. 1953. Animales salvajes de Chile en su clasificación moderna. Su vida y costumbres. Ediciónes de la Universidad de Chile, Santiago, 189 pp.
- HULL, D. 1973. Thermoregulation in young mammals. Pp. 167-200, in Comparative physiology of thermoregulation. Special aspects of thermoregulation (G. C. Whittow, ed.). Academic Press, New York, 3:1-278.
- JELINEK, P., L. VALICEK, B. SMID, AND R. HALOUZKA. 1978. Determination of papilomatosis in the coypus (Myocastor coypus Molina). Veterinarni Medicina (Prague), 23:113-119.
- KASUMOVA, N. I., S. I. RADJABLI, AND G. K. KULIEV. 1976. Cytogenetic investigation of nutria. I. Somatic and meiotic chromosomes of standard and white nutria. Genetika, 12:174-176 (in Russian).
- KATOMSKI, P. A., AND F. L. FERRANTE. 1974. Catecholamine content and histology of the adrenal glands of the nutria (Myocastor coypus). Comparative Biochemistry and Physiology, 48A:539-546.
- KAYS, C. E. 1956. An ecological study with emphasis on nutria (Myocastor coypus) in the vicinity of Price Lake, Rockefeller Refuge, Camorch Parish, Louisiana. M.S. thesis, Louisiana State University, Baton Rouge, 145 pp.
- KERR, R. 1792. The animal kingdom, or zoological system, of the celebrated Sir Charles Linnaeus. J. Murray and R. Faulder, London, 644 pp.
- KIM, P. 1980. The coypu. Myocastor coypus, in the Netherlands: reproduction, home range and manner of seeking food. Lutra, 23:55-64
- KLEIBER, M. 1961. The fire of life: an introduction to animal energetics. John Wiley and Sons, New York, 454 pp.
- KLEIMAN, D. G., J. F. EISENBERG, AND E. MALINIAK. 1979. Reproductive parameters and productivity of caviomorph rodents. Pp. 173-183, in Vertebrate ecology in the northern Neotropics (J. F. Eisenberg, ed.). Smithsonian Institution Press, Washington, 271 pp.
- 1956. Dojrzewanie i rozrod nutrii (Myocastor coypus). II. Jajnik. [Sexual maturation and reproduction in Myocastor coypus. II. The ovary.] Folia Biologica (Warsaw), 4:139-150.
- KOVALEV, V. L., R. K. ANDREEVA, AND S. N. STEPANOVA. 1978.

Wild animals as reservoirs of *Chlamydia*. Izdatel'stvo "Nauka," 1978:139-143.

- KUHN, L. W., AND E. P. PELOQUIN. 1974. Oregon's nutria problem. Vertebrate Pest Conference, 6:101-105.
- LAURIE, E. M. O. 1946. The coppu (Myocastor coppus) in Great Britain. Journal of Animal Ecology, 15:22-34.
   LAZARNS, A. B., AND F. P. Rowe. 1975. Freeze-marking rodents
- LAZARNS, A. B., AND F. P. ROWE. 1975. Freeze-marking rodents with a pressurised refrigerant. Mammal Review, 5:31-34.
- LINSCOMBE, G. 1976. An evaluation of the No. 2 Victor and 220 Conibear traps in coastal Louisiana. Proceedings of the Southeastern Association of Fish and Wildlife Agencies, 30:560– 568.
- LINSCOMBE, G., N. KINLER, AND V. WRIGHT. 1981. Nutria population density and vegetative changes in brackish marsh in coastal Louisiana. Pp. 129-141, in Proceedings of the worldwide furbearer conference (J. A. Chapman and D. Pursley, eds.). Worldwide Furbearer Conference Inc., Frostburg, Maryland, 1:1-651.
- LITJENS, B. E. J. 1980. De beverrat, Myocastor coypus (Molina), in Nederland. I. Het verloop van de populatie gedurende de periode 1963-1979. [The coypu, Myocastor coypus (Molina) in the Netherlands. I. Population development during the period 1963-1979.] Lutra, 23:43-53.
- LOMNICKI, A. 1957. Rytmika dobowa aktywnosci: nutrii Myocastor coypus Molina. [The daily rhythm of activity in the nutria *Myocastor coypus* Molina.] Folia Biologica (Warsaw), 5:293-306.
- LOPETEGUI, O. 1980. Observaciónes de la actividad anual de Myocastor coypus (Molina) en la Laguna de Malleco. Medio Ambiente (Universidad Austral de Chile, Valdivia), 4(2):29-34.
- LOWERY, G. H., Jr. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State University Press, Baton Rouge, 565 pp.
   MANN, G. F. 1978. Los pequeños mamíferos de Chile. Editorial
- Mann, G. F. 1978. Los pequeños mamíferos de Chile. Editorial de la Universidad de Concepción, Chile, 342 pp.
- Mann, T., and E. D. Wilson. 1962. Biochemical observations on the male accessory organs of nutria, *Myocastor coypus* (Molina). Journal of Endocrinology, 25:407-408.
- MARTIN, W. 1835. Visceral and osteological anatomy of the Coypus (Myopotamus Coypus, Comm.). Proceedings of the Zoological Society of London, 1835:173-182.
- MATOUCH, Ö., J. DONSEK, AND O. ONDRACEK. 1978. Vyskyt vztekliny u nutrie. [Rabies in the nutria.] Veterinarstvi, 28:549.
- MATTHIAS, K. E. K. 1941. Nutria. A profitable fur discovery. American Fur Breeder, July 1941:18-20.
- MICHALSKI, Z., AND W. SCHEURING. 1979. Kokcydioza jelit u nutrii [Coccidiosis of intestine in the nutria.] Wiadomosci Parazytologiczne, 25:99–104.
- MOLINA, G. I. 1782. Saggio sulla storia naturale del Chile. Stamperia di S. Tomnaso d'Aquino, Bologna (Italy), 367 pp.
- MORGAN, R. P., II, G. R. WILLNER, AND J. A. CHAPMAN. 1981. Genetic variation in Maryland nutria, Myocastor coypus. Pp. 30-37, in Proceedings of the worldwide furbearer conference (J. A. Chapman and D. Pursley, eds.). Worldwide Furbearer Conference Inc., Frostburg, Maryland, 1:1-651.
- MURUA, R., O. NEUMANN, AND I. DROPELMANN. 1981. Food habits of *Myocastor coypus* in Chile. Pp. 544-558, in Proceedings of the worldwide furbearer conference (J. A. Chapman and D. Pursley, eds.). Worldwide Furbearer Conference Inc., Frostburg, Maryland, 1:1-651.
- Newson, R. M. 1965. Reproduction in the feral coypu (Myocastor coypus). Journal of Reproduction and Fertility, 9:380-381.
- . 1966. Reproduction in the feral coypu (Myocastor coypus). Pp. 323-334, in Comparative biology of reproduction in mammals (I. W. Rowlands, ed.). Symposia of the Zoological Society of London, 15:1-559.
- . 1969. Population dynamics of the coypu, Myocastor coypus (Molina), in eastern England. Pp. 203-204, in Energy flows through small mammal populations (K. Petrusewicz and L. Ryszkowski, eds.). Polish Scientific Publishers, Warsaw, 350 pp.
- Newson, R. M., AND R. G. HOLMES. 1968. Some ectoparasites of the coypu (*Myocastor coypus*) in eastern England. Journal of Animal Ecology, 37:471-481.
- Norris, J. D. 1967. A campaign against feral coypus (Myocastor

- coypus Molina) in Great Britain. Journal of Applied Ecology, 4:191-199.
- NOWAK, R. M., AND J. L. PARADISO. 1983. Walker's mammals of the world. Fourth edition. The Johns Hopkins University Press, Baltimore, 2:569-1362.
- Oscood, W. H. 1943. The mammals of Chile. Field Museum of Natural History, Zoology Series, 30:1-268.
- PAGE, C. A., V. T. HARRIS, AND J. DURAND. 1957. A survey of virus in nutria. Southwest Lousiana Journal, 1:207-210.
- PALMISANO, A. W., AND H. H. DUPUIE. 1975. An evaluation of steel traps for taking fur animals in coastal Louisiana. Proceedings of the Southeastern Association of Game and Fish Commissioners, 29:342-347.
- PATTERSON, B., AND R. PASCUAL. 1968. New echimyid rodents from the Oligocene of Patagonia, and a synopsis of the family. Breviora, 301:1-14.
- PATTERSON, B., AND A. E. WOOD. 1982. Rodents from the Deseadan Oligocene of Bolivia and relationships of the Caviomorph. Bulletin of the Museum of Comparative Zoology, 149: 371-543.
- Peloquin, E. P. 1969. Growth and reproduction of the feral nutria *Myocastor coypus* (Molina) near Corvallis, Oregon. M.S. thesis, Oregon State University, Corvallis, 55 pp.
- PIETRZYK-WALKNOWSKA, J. 1956. Dojrzewanie i rozrod nutrii "Myocastor coypus." III. Jadro. [Sexual maturation and reproduction in the nutria Myocastor coypus. III. The testicle.] Folia Biologica (Warsaw), 4:151-162.
- POCOCK, R. I. 1922. On the external characteristics of some hystricomorph rodents. Proceedings of the Zoological Society of London, 1922:365-427.
- ROBICHEAUX, B. L. 1978. Ecological implications of variably spaced ditches on nutria in a brackish marsh, Rockefeller Refuge, Louisiana. M.S. thesis, Louisiana State University, Baton Rouge, 49 pp.
- ROVERETO, G. 1914. Los estratos araucanos y sus fosiles. Anales del Museo Nacional de Historia Natural de Buenos Aires, 25: 1-247.
- ROWLANDS, I. W., AND R. B. HEAP. 1966. Histological observations on the ovary and progesterone levels in the coypu (Myocastor coypus). Pp. 335-352, in Comparative biology of reproduction in mammals (I. W. Rowlands, ed.). Symposia of the Zoological Society of London, Academic Press, New York, 15:1-559.
- RYSZKOWSKI, L. 1966. The space organization of nutria (Myocastor coypus) populations. Symposia of the Zoological Society of London, 18:259-265.
- SACHER, G. A., AND E. F. STAFFELDT. 1974. Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth. American Naturalist, 108: 593-615.
- SAFAROV, Y. B., AND M. A. KURBANOVA. 1976. Influence of some therapeutic substances on the immulogical response of nutria *Myocastor coypu* (antibiotics and nitrofurans in relation to salmonellosis). Veterinariya (Moscow), 11:65-66 (in Russian).
- Scheuring, W., and E. Bratkowska. 1976. Hematological values in nutria. Medycyna Weterynaryjna, 32:239-241.
- SCHEURING, W., AND J. A. MADEJ. 1976. Sarcosporidiosis in nutria. Medycyna Weterynaryjna, 32:437-438.
- Schitoskey, F., Jr., J. Evans, and G. K. Lavoie. 1972. Status and control of nutria in California. Vertebrate Pest Conference, 5:15-17.
- SEGAL, A. N. 1978. Thermoregulation in *Myocastor coypus* in summer. Zoologicheskii Zhurnal, 57:1878-1883.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, 85:1-350.
- SKOWRON-CENDRZAK, A. 1956. Dojrzewanie i rozrod nutrii "Myocastor coypus." I. Cyklplciowy. [Sexual maturation and reproduction in Myocastor coypus. I. The oestrus cycle.] Folia Biologica (Warsaw), 4:119-138.
- SLIPPER, E. J. 1958. Organ weights and symmetry problems in porpoises and seals. Archives Neerlandaises de Zoologie, 13: 97-113.
- . 1962. Whales. Hutchinson and Company, London, 475
- SPOTORNO, A. O. 1979. Contrastacion de la macrosistemática de roedores caviomorfos por analisis comparativo de la morfologia

reproductiva masculina. Archivos de Biológia y Medicina Experimentales, 12:97-106.

SZYNKIEWICZ, E. 1968. Studies on antigenic differentiation of blood in the coypu (Myocastor coypu Molina, 1792). European Conference on Animal Blood Groups and Biochemical Polymorphism, 9:567-570.

8

- ——. 1971. Investigations on differentiation of beta-globulin subfractions in the blood serum of nutria (Myocastor coypus Molina, 1792). Genetica Polinica, 12:465.
- TALBERT, R. E. 1962. Control of nutria. California Department of Agriculture Bulletin, 51:156-157.
- TSIGALIDOU, V., A. G. SIMOTAS, AND A. FASOULAS. 1966. Chromosomes of the coypu. Nature, 211:994-995.
- TWICC, G. I. 1973. Rat-bone leptospirosis in wildlife and on the farm. Mammal Review, 3:37-42.
- VALENTINE, J. M., JR., J. R. WALTHER, K. M. McCartney, and L. M. Ivy. 1972. Alligator diets on the Sabine National Wildlife Refuge, Louisiana. The Journal of Wildlife Management, 36: 809–815.
- WAGNER, J. A. 1963. Gross and microscopic anatomy of the digestive system of the nutria, Myocastor coypus bonariensis (Geoffrey). Journal of Morphology, 112:319-333.
- WARKENTIN, M. J. 1968. Observations on the behavior and ecology of the nutria in Louisiana. Tulane Studies in Zoology and Botany, 15:10-17.
- Weir, B. J. 1974. Reproductive characteristics of hystricomorph rodents. Symposia of the Zoological Society of London, 34: 265-301.
- WENTZ, W. A. 1971. The impact of nutria (Myocastor coypus) on marsh vegetation in the Willamette Valley, Oregon. M.S. thesis, Oregon State University, Corvallis, 41 pp.
- WESMAEL, C. 1841. Bulletin de l'Academie Royale de Medecine de Belgique, 8:59-61.
- WEST, G. B. 1955. The comparative pharmacology of the suprarenal medulla. The Quarterly Review of Biology, 30:116– 137.
- WILLNER, G. R. 1982. Nutria: Myocastor coypu. Pp. 1059– 1076, in Wild mammals of North America (J. A. Chapman and G. A. Feldhamer, eds.). The Johns Hopkins University Press, Baltimore, 1147 pp.
- WILLNER, G. R., J. A. CHAPMAN, AND D. PURSLEY. 1979. Reproduction, physiological responses, food habits, and abundance of nutria on Maryland marshes. Wildlife Monographs, 65:1–43.
- WILLNER, G. R., K. R. DIXON, J. A. CHAPMAN, AND J. R. STAUFFER, JR. 1980. A model for predicting age-specific body weights of nutria without age determination. Journal of Applied Ecology, 7:343-347.

- WILSON, E. D., AND A. A. DEWEES. 1962. Body weights, adrenal weights and oestrous cycles of nutria. Journal of Mammalogy, 43:362-364.
- WILSON, E. D., M. X. ZARROW, AND H. S. LIPSCOMB. 1964. Bilateral dimorphism of the adrenal glands in the coypu (Myocastor coypus, Molina). Endocrinology, 74:515-517.
- WOLFE, J. L., D. K. BRADSHAW, AND R. H. CHABRECK. 1987.
  Alligator feeding habits: new data and a review. Northeast Gulf Science, 9:1-8.
- WOOD, A. E., AND B. PATTERSON. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. Bulletin of the Museum of Comparative Zoology, 120:279-428.
- Woons, C. A. 1972. Comparative myology of jaw, hyoid, and pectoral appendicular regions of New and Old World hystricomorph rodents. Bulletin of the American Museum of Natural History, 147:115-198.
- . 1976. How hystricognath rodents chew. American Zoologist, 16:215.
- ——. 1982. The history and classification of South American hystricognath rodents: reflections on the far away and long ago. Pp. 377-392, in Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publications Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, 539 pp.
- ——. 1984. Hystricognath rodents. Pp. 389-446, in Orders and families of recent mammals of the world (S. Anderson and J. K. Jones, Jr., eds.). John Wiley and Sons, New York, 686 pp.
- WOODS, C. A., AND E. B. HOWLAND. 1977. The skin musculature of hystricognath and other selected rodents. Zentralblatt fur Veterinaermedizin Reihe C. 6:240-264.
- ——. 1979. Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. Journal of Mammalogy, 60:95– 116
- Editors of this account were B. J. Verts, Troy L. Best, Guy N. Cameron and Sydney Anderson. Managing Editor was Craig S. Hood.
- C. A. Woods, Florida Museum of Natural History, Gainesville, Florida 32611; L. Contreras, Avenida Las Perdices 0571-17, La Reina, Santiago, Chile; G. Willner Chapman, Department of Fish and Wildlife, Utah State University, Logan, Utah 84322; H. P. Whidden, Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01002.